AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 104:177–192 (1997)

Genetic Structure of the Indigenous Populations of Siberia

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KEY WORDS indigenous Siberians; spatial autocorrelation; R-matrix; DNA VNTRs; Mantel tests

ABSTRACT This study explores the genetic structure of Siberian indigenous populations on the basis of standard blood group and protein markers and DNA variable number of tandem repeats (VNTR) variation. Four analytical methods were utilized in this study: Harpending and Jenkin's R-matrix; Harpending and Ward's method of correlating genetic heterozygosity (H) to the distance from the centroid of the gene frequency array (r_{ii}); spatial autocorrelation, and Mantel tests. Because of the underlying assumptions of the various methods, the numbers of populations used in the analyses varied from 15 to 62. Since spatial autocorrelation is based upon separate correlations between alleles, a larger number of standard blood markers and populations were used. Fewest Siberian populations have been sampled for VNTRs, thus, only a limited comparison was possible. The four analytical procedures employed in this study yielded complementary results suggestive of the effects of unique historical events, evolutionary forces, and geography on the distribution of alleles in Siberian indigenous populations. The principal components analysis of the R-matrix demonstrated the presence of populational clusters that reflect their phylogenetic relationship. Mantel comparisons of matrices indicate that an intimate relationship exists between geography, languages, and genetics of Siberian populations. Spatial autocorrelation patterns reflect the isolation-by-distance model of Malecot and the possible effects of long-distance migration. Am J Phys Anthropol 104:177–192, 1997.

Siberia is an expansive landmass stretching from the Ural mountains of the west to the Pacific coast of the east. It is populated by indigenous peoples scattered throughout a diverse and often harsh environment which includes the arctic tundra and subarctic taiga of the north, and the mountainous and semi-arid grassland regions of the south. The languages spoken by these indigenous populations are classified into three major linguistic groups-Altaic, Uralic, and Paleoasiatic (Ruhlen, 1976) (see Table 1).

In Siberia the Altaic family, consists of three branches: Turkic, Mongolic, and Tungus-Manchu (Shirokogoroff, 1970). Turkic languages are distributed primarily along the southern edge of Siberia, except for the Yakut language which is found in northeastern Siberia in the form of a "wedge" between Evenki settlements and following the basin

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Received 15 April 1996; accepted 9 August 1997.

Contract grant sponsor: NSF, Grant numbers BNS 576-11859 and BSR 910-1571; Contract grant sponsor: General Research Fund of the University of Kansas.

TABLE 1. Siberian indigenous languages and ethnic group (after Karafet, 1997)*

Language family	Ethnic group	Size[1]
Altaic		
Turkic	Altais (Altays)[2]	57,000
	Chelkanians (Chelkans)	
	Kumandinians (Kumandin)	
	Tuvans (Touvins)	139,000
	Tofalars (Tubalars)	720
	Yakuts	296,000
Mongolic	Buryats	314,000
Tungus-Manchu		
Tungusic	Evens (Lamuts)	17,000
	Evenks	29,900
Manchu	Udehe (Udegey)	1,900
	Nanais (Gol'dy)	11,900
	Ul'chi	3,200
Uralic		
Samoyedic	Entsi (Enets)	190
	Nentsi (Nenets)	34,200
	Ngansans	1,300
	Selkups (Sel'kupi)	3,600
Ugric	Khants (Ostyaks)	22,300
	Mansi (Voguls)	8,300
Paleoasiatic		
Chukotko-Kamchatkan	Chukchi	15,100
	Itel'mens (Kamchadals)	2,400
	Koryaks	8,900
Eskimo-Aleut	Eskimos	1,700
	Aleuts	650
Isolates	Kets (Yenisey Ostyaks)	1,080
	Nivkhs (Gilyaks)	4,600

[1] Census-based numerical information.
[2] Alternate names and spellings for these groups are shown in (parentheses). This variation in the English spelling of the tribal names reflects the transcription from Cyrillic orthography to Roman.
* Unpublished manuscript.

of the middle Lena and lower Aldan rivers (see Szathmary, 1981). During historic times the Yakuts expanded from the south into this northerly location (Levin and Potapov, 1964). The Mongolic branch of the Altaic language family is spoken by the Buryats who are dispersed around Lake Baykal (Vyatkina, 1964). The Tungus-Manchu languages are spoken by the inhabitants of northern Siberia, including the Evenki, Eveni, and Negidal. The Manchu speakers (Nanai, Orochi, and Ul'chi) reside in the lower basin of the Amur River and the Maritime District of Far Eastern Siberia. Szathmary (1981) briefly summarized the literature on the linguistic and geographic distribution of arctic and subarctic indigenous populations of Siberia.

The Uralic language family includes the Finno-Ugric and Samoyedic branches (Ruhlen, 1976). These languages are distributed throughout northwestern Siberia with Ugric spoken by Khants and Mansi, while Samoyedic languages are spoken by the Nganasans, Sel'kups, Nentsi, and Entsi (Khonti, 1985).

Paleoasiatic or Paleosiberian is a heterogenous group of languages that may share some distinguishing linguistic features (such as uvular stops and a case system) (Ruhlen, 1976). They are thought to be the most ancient of the Siberian languages that fail to fit into the two major linguistic families. The speakers of Paleoasiatic are geographically dispersed throughout northeastern Siberia. Isayev (1977) has argued that the Paleoasiatic languages can be subdivided into three groups that share some common linguistic features. Populations such as the Chukchi, Itelmeni, Koryaks share linguistic features and have been included in the Chukchi-Kamchatkan (also known as Chukotko-Kamchatkan) linguistic group (Ruhlen, 1976). Eskimos (Yupik and Inupik) and Aleuts are often grouped together and included in the Paleoasiatic languages. The third category has been termed "language isolates," consisting of two languages (Ket and Nivkh) that do not appear to be related to any of the other Paleoasiatic linguistic groups (Ruhlen, 1976). Rogers (1986) hypothesized that much of the observed linguistic variation of the tribal populations of Siberia can be attributed to their geographic isolation during the Pleistocene. A massive ice sheet and an inland sea in central Siberia formed a physical barrier to east-west population movement and may have led to the linguistic microdifferentiation of Uralic, Altaic, and Paleosiberian populations.

The genetic structure of indigenous populations of Siberia has been investigated since the late 1960s and early 1970s (Rychkov, 1965; 1969; Rychkov and Sheremet'eva, 1972; Szathmary, 1981). Earlier genetic studies of Siberian groups tended to be descriptive surveys of blood group frequency distributions in indigenous groups (Levin, 1958; Spitsin, 1967; Zolotareva, 1968). By contrast, Rychkov attempted to fit deterministic models of migration and selection, al-

TABLE 2. Siberian and New World populations studied and their approximate geographical coordinates

Index population	Group	Longitude	Latitude
1 Beryozovka	Evens	158°00′E	67°00′N
2 Sebyan-Kuyhel	Evens	132°00′E	66°00′N
3 Andryushkino	Evens	154°00′E	69°00′N
4 Avamskaya	Nganasan	93°00′E	72°00′N
5 Tamirskaya	Nganasan	95°00′E	72°00′N
6 Vadeyskaya	Nganasan	102°00′E	72°00′N
7 FN-Sytomino (CM)	Forest Nentsi	72°00′E	62°00′N
8 FN-Numto Lake (HT)	Forest Nentsi	71°00′E	63°00′N
9 FN-Tarko-Sale (TC)	Forest Nentsi	78°00′E	65°00′N
10 FN-Vangapur (VP)	Forest Nentsi	77°00′E	64°00′N
11 FN-Kharampur (MII)	Forest Nentsi	78°00′E	64°00′N
12 FN-Khalyasoway (MV)	Forest Nentsi	78°00′E	63°00′N
13 FN-Varyogan (VN)	Forest Nentsi	77°00′E	62°00′N
14 Vayegi	Reindeer Chukchi	172°00′E	64°00′N
15 Ust-Belayan	Reindeer Chukchi	174°00′E	66°00′N
16 Ryt-Kychi	Reindeer Chukchi	171°00′E	67°00′N
17 Ryt-Kaipiy	Reindeer Chukchi	178°00′E	67°00′N
18 Amgyema	Reindeer Chukchi	180°00′E	67°00′N
19 Kanchalan	Reindeer Chukchi	178°00′E	66°00′N
20 Alkatwaam	Reindeer Chukchi	178°00′E	63°00′N
21 Menipel	Reindeer Chukchi	177°00′E	62°00′N
22 Achaivayam	Reindeer Chukchi	171°00′E	61°00′N
23 Sredny	Reindeer Chukchi	169°00′E	61°00′N
24 Chaplino	Asian Eskimo	172°00′W	64°30′N
25 Siryeniki	Coastal Chukchi	174°00′W	64°30′N
26 Naykan	Asian Eskimo	170°00′W	66°00′N
27 Uelen	Asian Eskimo	179°30′W	65°30′N
28 Savoonga	Yupik Eskimo	171°00′W	63°00′N
29 Gambell	Yupik Eskimo	173°00′W	63°00′N
30 Wales	Inupik Eskimo	168°00′W	66°00′N
31 King Island	Inupik Eskimo	168°00′W	65°00′N
32 Aleuts: St. Paul	Pribilof I. Aleuts	171°00′W	57°10′N
33 Aleuts: St. George	Pribilof I. Aleuts	169°00′W	56°30′N
34 KIE: Old Harbor	Kodiak Island Eskimo	153°00′W	57°00′N
35 KIE: Ouzinkie	Kodiak Island Eskimo	151°00′W	58°00′N
36 KIE: Larsen Bay	Kodiak Island Eskimo	154°00′W	57°30′N
37 KIE: Akhiok	Kodiak Island Eskimo	154°30′W	57°00′N
38 Ratta	Sel'kups	84°00′E	63°00′N
39 Tolka upon Taz	Sel'kups	82°00′E	64°00′N
40 Bering Island	Commander I. Aleuts	166°00′E	55°00′N
41 Mednii	Commander I. Aleuts	168°00′E	53°00′N
42 Suronash	Chelkanians	88°00′E	52°20′N
43 Kurmach-Baygol	Chelkanians	87°30′E	52°20′N
44 May	Chelkanians	88°10′E	52°20′N
45 Shunarak & Kubiya	Kumandinians	86°30′E	52°30′N
46 Ozerki & Yegona	Kumandinians	86°00′E	52°10′N
47 Suduntui	Buryats	115°00′E	52°00′N
48 Sakhurta	Buryats	115°00′E	51°00′N
49 Ust-Orda	Buryats	105°00′E	54°00′N
50 Olhon	Buryats	108°00′E	54°00′N
51 Mogsohon	Buryats	110°00′E	53°00′N
52 Surinda	Evenks	97°20′E	62°40′N
53 Poligus	Evenks	94°40′E	63°20′N
54 Sulamai Kets	Kets	90°30′E	61°30′N
56 Udehe	Eastern Evenks	137°30′E	48°50′N
57 Ulan Bator	Mongolian	106°30′E	48°00′N
58 Goutara	Tofalars	96°30′E	53°30′N
59 Nerkha	Tofalars	97°30′E	53°20′N
60 Alygdzher	Tofalars	97°40′E	53°15′N
61 Todzha	Touvin	95°30′E	52°30′N
62 Touva	Touvin	96°30′E	52°20′N

though sometimes without sufficient invocation of stochastic processes expected in the small Arctic and sub-Arctic populations. He "painted" the genetic landscape of the circumpolar region with broad strokes using sketchy gene frequency data in the construction of his models (Rychkov and Sheremet'eva, 1980).

The few attempts at the reconstruction of the genetic structure of circumpolar populations (e.g., Crawford et al., 1981; Crawford and Encisco, 1982) were based upon a melange of field investigations among New World populations (e.g., Inuit), with the compilation of gene frequencies from Russian sources. Although the analyses of the Eskimo populations were based on large arrays of genetic markers, comparable gene frequency data for Siberian groups were often unavailable. As a result, the analyses of 52 circumpolar populations (Crawford and Enciso, 1982) were based on only three blood group loci (ABO, MN and RH). Unfortunately, an inverse relationship exists between the number of loci for which data are available and the number of possible populations (Crawford and Enciso, 1982).

Since the late 1970s, a larger number of genetic markers and new analytical techniques have been applied to the characterization of the genetic structure of Siberian indigenous populations. In addition to the standard genetic distances, dendrograms, and R-matrix analyses, Sokal introduced spatial autocorrelation methods for the study of the geographic distribution of human genes (Sokal and Friedlaender, 1982). Cavalli-Sforza and his colleagues documented the effects of human demic expansions on allelic frequency distributions using synthetic gene maps (Menozzi et al., 1978). The introduction of Mantel tests, partial correlations and multiple correlations between matrices has permitted further statistical explorations of the interactions between geography, genetic and linguistic variation (Crawford and Duggirala, 1992) (see Table 4).

This paper examines: (1) the genetic relationships among Siberian populations and the relative roles of languages and geography in explaining the observed genetic variation; (2) the concordance of the results from four different analytical methods (R-matrix analysis, H vs. r_{ii}, Mantel tests, and spatial autocorrelation) applied to frequencies of standard genetic markers and whenever possible—DNA VNTRs.

METHODS

Allelic frequencies were compiled from a number of different studies and publications (Majumder et al., 1988; Posukh et al., 1990; Karaphet and Osipova (1993), Sukernik et al. (1978, 1982); Sukernik and Osipova (1982); Crawford et al. (1981); and Crawford et al., unpublished data). Frequencies for ABO*A, MN*M, MN*N, and RH*d have been derived for some populations by summing over allele variants, e.g., the frequencies of ABO*A1 and ABO*A2 were summed in some populations to obtain a frequency for ABO*A. This summation was necessitated because, due to the scarcity of antisera, few populations have been characterized for some of the variant alleles. The loci, alleles, and number of populations and their locations (latitude and longitude) for which data were available are listed in Tables 2 and 3.

R-matrix analysis

The R-matrix is a topological approach of representing population structure (Harpending and Jenkins, 1973). An **R,** or relationship matrix is constructed utilizing allelic frequencies of subdivisions of a population. The relative relationships among the groups in the sample are represented graphically in two or three dimensions by an eigenvectorial reduction of the covariance matrix. For the application of this method to the analysis of the genetic structure of circumpolar populations see Crawford et al. (1981) and Crawford and Enciso (1982).

Heterozygosity and distance

Harpending and Ward (1982) developed a method that permits an estimation of the relative roles of systematic vs. nonsystematic pressures on the differentiation of subdivided populations. Given uniform systematic pressure, genetic heterozygosity (H) is negatively correlated with genetic distance from the centroid of the gene frequency array (r_{ii}). Systematic gene flow and admixture are reflected in the higher levels of heterozygosity than predicted by regression on r_{ii}. Conversely, populations experiencing genetic drift have higher r_{ii} values and low heterozygosity.

Mantel statistics

Statistical comparisons of matrices permit the examination of the relationship

TABLE 3. Loci and alleles examined, and number of populations for which allele frequency data were available

Locus	Allele	n	Locus	Allele	n
ABO	A1	46	JK	Jka	10
	A2	26		Jkb	4
	A	15			
	B	61	DI	Dia	28
	O	61		Dib	28
	⟨A⟩	61			
			HPA	Hp1	45
MNS	M	11		Hp2	38
	N	11			
	MS	49	PGM	PGM1-1	49
	Ms	49		PGM2-2	42
	NS	49			
	Ns	49	6PGD	PGD-A	46
	⟨M⟩	60		PGD-C	39
P	P1	43	AK	AK1	21
	P2 + p	36		AK2	14
RH	CDE (Rz)	23	ACP1	Pa	44
	CwDE (Rzw)	5		Pb	44
	CDe (R1)	55		Pc	21
	CwDe (R1w)	15			
	CdE (ry)	14	GM	za;g	36
	Cde (r′)	11		zax;g	36
	cDE (R2)	55		za;b035st	36
	cDe (R0)	44		f;b0135	36
	cdE (r″)	9			
	cde (r)	39	KM	Km1	27
	⟨d⟩	61		Km2	10
FY	Fya	44			
	Fyb	38			
KEL	K	27			
	k	20			
	Kpa	16			
	Kpb	9			

Frequencies for alleles in angle brackets (⟨ ⟩) were derived from the reported allele frequencies.

among genetics, geography and linguistics in human populations. Given two distance matrices **A** and **B,** Mantel (1967) tests examine an association between their elements by using the statistic

$$\mathbf{Z}_{AB} = \sum_{ij} \mathbf{A}_{ij}\, \mathbf{B}_{ij}$$

where A_{ij} and B_{ij} are elements of row i and column j of matrices **A** and **B,** which results in an unnormalized correlation coefficient. The statistic $\mathbf{Z}_{AB}$ is normalized into a product-moment correlation coefficient that ranges from −1 to +1. The significance of correlations is tested by comparing the observed correlations against a sampling distribution of **Z** based on a randomized **B** matrix B_R.

In this analysis of Siberian indigenous populations, interactions between genetics (as measured by Harpending and Jenkins distances, d_{ij}^2), geography (computed as great circle distances), and linguistics (distances based on the hierarchical structure of the branching of the Siberia languages) were examined using Mantel tests. A linguistic distance matrix was constructed on the basis of scores assigned to reflect the hierarchical structure of the languages differences. For example, a score of 4 was given if the language difference was at the family level (Altaic, Paleosiberian, and Isolated languages). Thus, the distance from Yakuts to Kets was 4. A score of 3 was given if the language difference was at the subfamily level. For example, the distance of 3 was assigned from Yakuts (Turkic) to Evens (Tungusic). Scores of 2 were given to language differences at the branch level, e.g., the distance between Eskimo Yupik and Inupik. A score of 1 was assigned to groups belonging to the same branch, e.g., Coastal Chukchi and Reindeer Chukchi.

TABLE 4. Correlations of genetic (GENE), geographic (GEOG), and linguistic (LING) distance matrices

	Correlation (r)	p[1]
(1) Correlations:		
Distances compared		
GENE ∗ GEOG	0.546	0.001
GENE ∗ LING	0.351	0.001
GEOG ∗ LING	0.500	0.001
(2) Partial Correlations[2]:		
Test of relationship		
GENE ∗ GEOG (LING)	0.456	0.001
GENE ∗ LING (GEOG)	0.108	0.152
(3) Multiple Correlations[3]:		
Test of relationship		
GENE ∗ GEOG, LING	0.553	0.001

[1] Mantel test probabilities.
[2] Partial correlations between two matrices influencing the third matrix.
[3] Multiple correlation obtained through multiple regression of genetic distance matrix against both geographic and linguistic distance matrices.

Spatial autocorrelation analysis

One method of exploring spatial patterning in variate values and of gaining insight into the processes which structure these variates in space is spatial autocorrelation analysis (Cliff et al., 1975; Haggett et al., 1977; Cliff and Ord, 1973, 1981; Sokal and Oden, 1978a,b; Glick, 1979; Cliff et al., 1981). Here, spatial autocorrelation analysis of allelic frequency data is used to elucidate continental-scale patterns of population

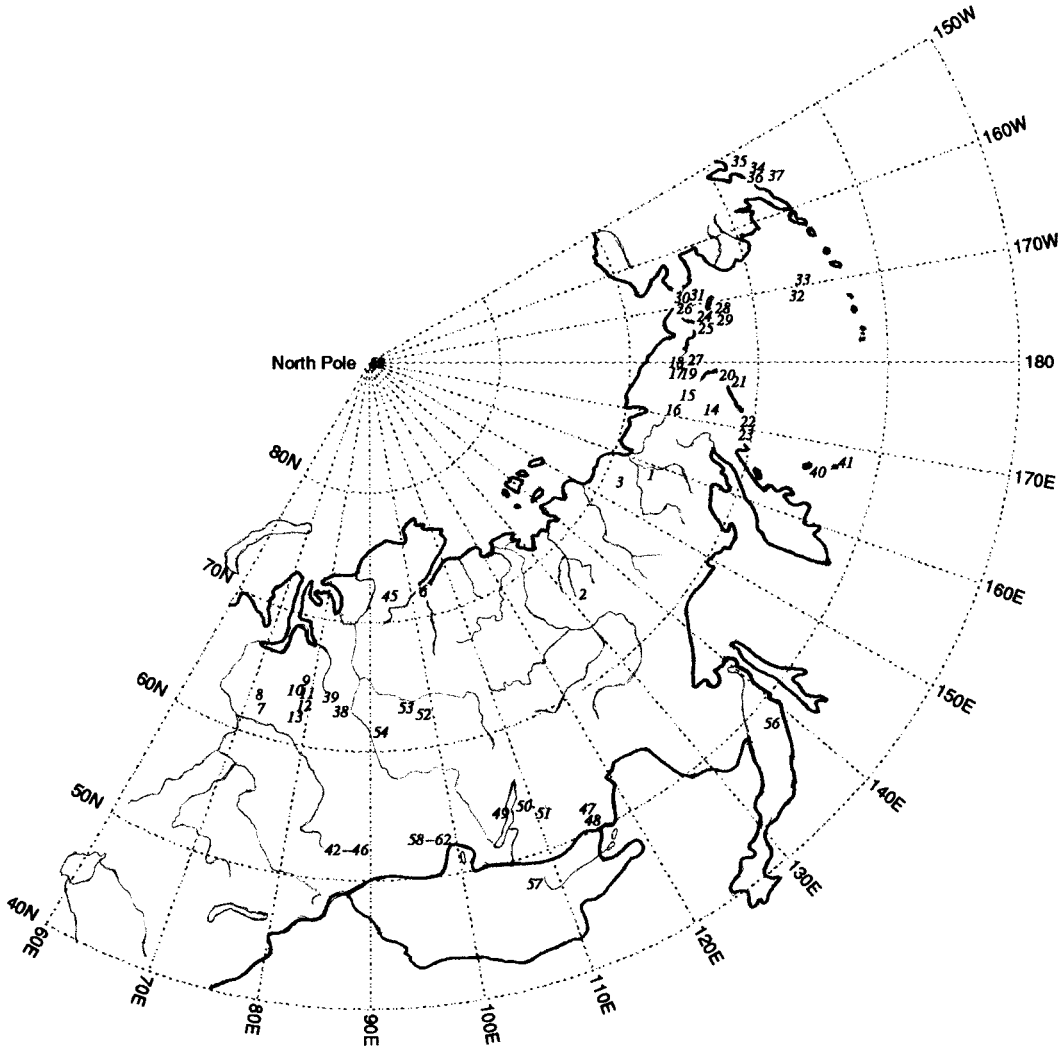

Fig. 1. Map of Siberia indicating the geographic locations of the indigenous populations whose allelic frequencies were used for various analyses of structure. The numbers of the populations located in this map correspond to those listed in Table 3.

structure among 61 contemporary Siberian, Aleutian, and Alaskan Eskimo populations.

The data for the spatial autocorrelation analysis consist of the geographical locations (latitude and longitude) of 61 Siberian and New World (Aleutian and Alaskan) populations, and as many as 50 allele frequencies for each population (Table 3). The populations represent 19 ethnic subdivisions; 15 loci are surveyed by the allelic frequencies.

Longitude and latitude for each population were estimated from maps of the region. For populations that are dispersed and occupy relatively large territories, the coordinates given in Table 2 are estimates of the geographic centroid of the population distribution. The populations are distributed in a roughly annular pattern surrounding the Sea of Okhotsk and the mountainous lands to the north, between the Sea of Okhotsk and the East Siberian Sea (see Fig. 1). Distances among the populations range from 12 to 6742 kms, with a median distance of 2815 kms. Because of the annular distribu-

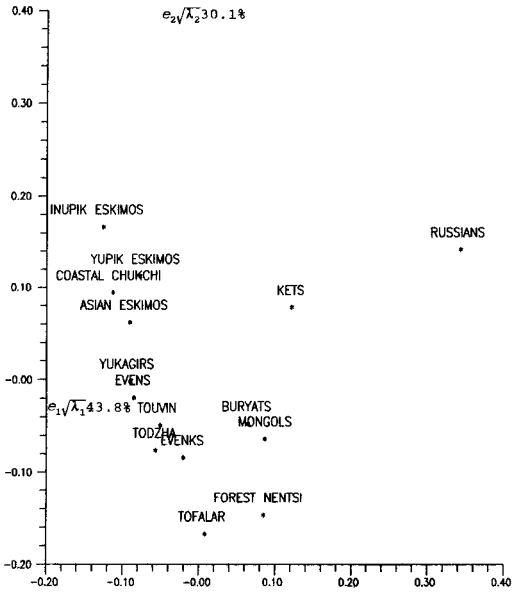

Fig. 2. A true least squares reduction of an R-matrix into a "genetic map" consisting of a plot between the first and second axes of 15 populations and 7 genetic loci. The two scaled eigenvectors account for more than 74% of the total variance.

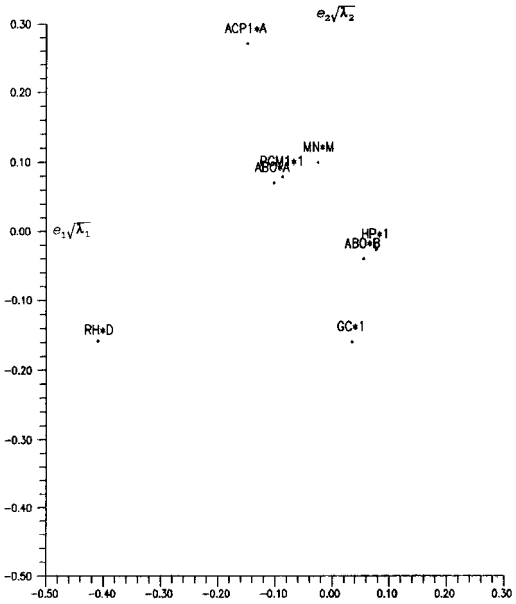

Fig. 3. Distribution of the alleles plotted along the first two scaled eigenvectors for the 15 populations shown in Fig. 2.

tion of the populations, the distribution of the interpopulational distances is strongly bimodal, with peaks at 1300 and 4500 kms.

In the spatial autocorrelation analysis, allelic frequencies received uniform weighting because of the considerable variation in the reporting of these data. For example, the variances of allelic frequencies are not always provided, neither are the sample sizes involved in the frequency estimates. There is also wide variation in the allelic frequencies actually reported, especially among those systems with variant alleles.

Spatial autocorrelation analysis and correlogram construction were performed according to the procedures in Cliff and Ord (1981). Moran's **I** (as opposed to Geary's **c**) was chosen as the coefficient of spatial autocorrelation because of its numerical and statistical properties (Cliff and Ord, 1973, 1981; Haggett et al., 1977). Initially the data were analyzed with binary (0/1), inverse-distance ($\mathbf{d}^{-1}$), and inverse-squared distance ($\mathbf{d}^{-2}$) weighting functions (all distances between populations were measured along great-circle routes). The correlograms obtained under each weighting scheme were nearly identical, however, differing slightly in the magnitude of the autocorrelation coefficient at the smallest spatial lag, and only the results obtained with an inverse-distance ($\mathbf{d}^{-1}$) weighting function are presented here.

The appearance of a spatial correlogram depends to some extent on the number of spatial lags (distance classes) used in its construction, although the exact number of lags is not usually critical within a certain range. Ten spatial distance classes were utilized in this analysis, although the patterns were found to be robust to variation in the number of spatial lags from 6 to 14. Because of the strongly bimodal character of the distribution of distances between populations, the spatial lags in the correlograms are spaced uniformly in data rather than uniformly in distance.

RESULTS

R-matrix

Figure 2 is a true-least squares reduction of an R-matrix into a "genetic map" based on 15 populations, 7 loci (ABO, MN, RH, HP,

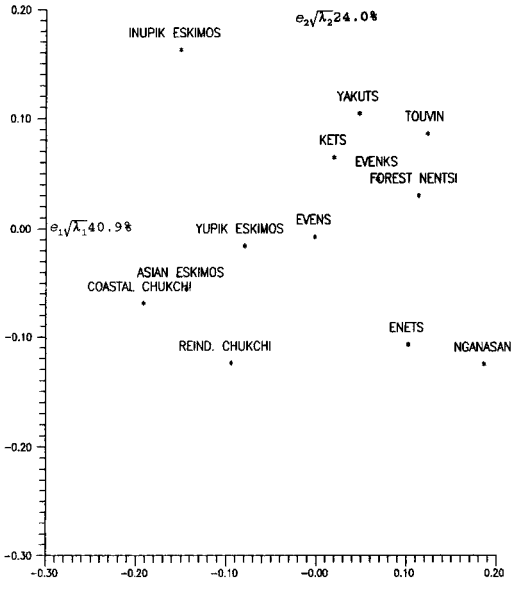

Fig. 4. Plot of the relationship between 13 populations, including 11 Siberian and 2 North American groups, reduced by least-squares from 9 alleles into two dimensions. The total variance subsumed by the first two eigenvectors is 65%.

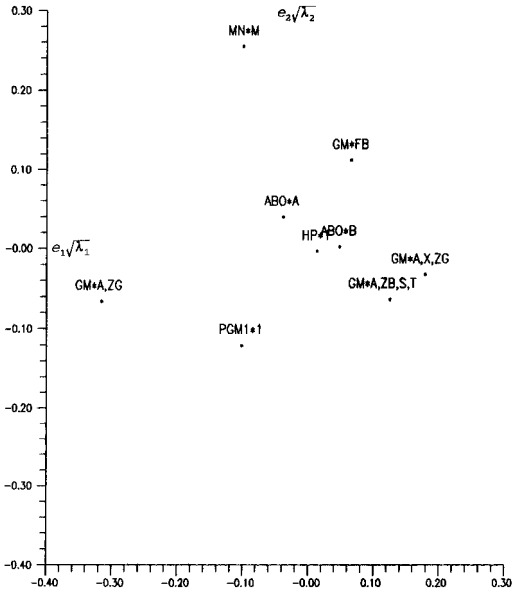

Fig. 5. Distribution of the nine alleles dispersed along the first two scaled eigenvectors in the genetic plot shown in Fig. 4.

ACP1, PGM1, GC) and 8 alleles. This plot of the first versus the second scaled eigenvectors explains more than 74% of the total variance. The first axis separates the Russian sample from the indigenous Siberian and Mongol populations. The second axis clusters the Paleo-Asian speakers some distance from the Samoyed and Turkic speakers. The Buryats align closely with the Mongols while the Yukagirs are proximal to the Evens. This affinity of the Evens and Yukagirs reflects the recent gene flow between them as shown in the study of Posukh et al. (1990). The Turkic-speaking populations, i.e., Todzhans, Touvans (Touvins), and Tofalars do not form distinct clusters but instead show affinity for the Evenki and Nentsi. It is unclear whether the R-matrix plot reveals some genetic structure, not apparent from historic and linguistic reconstructions, or whether these groups were not sampled adequately. The addition of GM haplotype frequencies to an R-matrix analysis (see Fig. 3), brings the Touvans closer to the Yakuts, as would be expected from two Turkic groups.

Figure 2 provides a plot of the distribution of the alleles along the first two scaled eigenvectors for the 15 populations shown in the genetic map of Fig. 3. The Russian sample was separated from the indigenous Siberian populations by the low frequencies of the RH*D and the concomitant high frequency of RH*d. Only RH*D is plotted in Fig. 3, because the frequency of the RH*d is not independent of RH*D thus using both alleles in this analysis would introduce redundancy of information. If the frequency of RH*R (d) in the indigenous populations is diagnostic of gene flow from Russians, then the Ket sample from Sulamai contains the most Russian admixture. The separation of the Paleo-Asiatic groups is primarily due to the relatively high frequencies of ACP1*A allele and low frequency of GC*1.

Figure 4 is a genetic map of 13 populations based upon 5 loci (ABO, MN, HP, PGM1, and GM), and 9 alleles. Because so few Siberian populations have been characterized by GM haplotypes, we are limited to 13 populations and 5 genetic loci. However, Schanfield (1980) has argued that the GM are the most highly informative system in discriminating between populations. The total variance subsumed by the first and second axes is 65%, slightly lower than found in

our analysis based upon 7 loci and 15 populations (see Fig. 2). The first axis separates the Paleo-Asiatic speaking groups from the Samoyedic groups and the remaining populations. Since there are no Russian populations included in Fig. 4, the first eigenvector is in a different direction from the plot shown in Fig. 2. The second axis explains the separation of the Inupik Eskimos of Alaska from the remaining populations. The two Turkic aggregates, the Yakuts and Touvans clearly exhibit their southern origins by clustering close together. The Coastal Chukchi are located between the Asian Eskimos and the Reindeer Chukchi again documenting the gene flow between these groups in coastal settlements.

As indicated in Fig. 5, the dispersal of the Paleo-Asian groups is due to the high incidence of the GM*A G (GM*A,ZG) haplotype and PGM1*1 allele. The PGM1*1 allele is particularly frequent in the two Chukchi groups. The Alaskan Inupik groups are separated from the other groups by the high frequency of MN*M allele. The Enetsi and Nganasans can be distinguished from other Siberian groups by the high frequency of GM*X G (GM*A,X,ZG) among the Entsi (Enets) and GM*A T (GM*A,ZB,S,T) among the Nganasans.

Heterozygosity and r_{ii}

Figure 6 provides a plot of the regression between r_{ii} values and mean per locus heterozygosity. The regression line shown is the theoretical one (see Fig. 6). This plot indicates that the Eskimo and Chukchi groups are distinct from other Siberian populations and according to their low heterozygosity levels (associated with below average external gene flow) and genetic isolation from the other groups. The Inupik Eskimos, in this case, from Wales, Alaska, are members of a highly isolated, small population of approximately 120 residents. The Wales sample exhibits the highest r_{ii} and lowest heterozygosity values. On the other hand, Forest Nentsi display the highest level of heterozygosity but intermediate r_{ii} values, probably indicative of the collective action of gene flow and reproductive isolation. The Kets exhibit high heterozygosity but low levels of r_{ii} which in Fig. 2 shows their intermediate

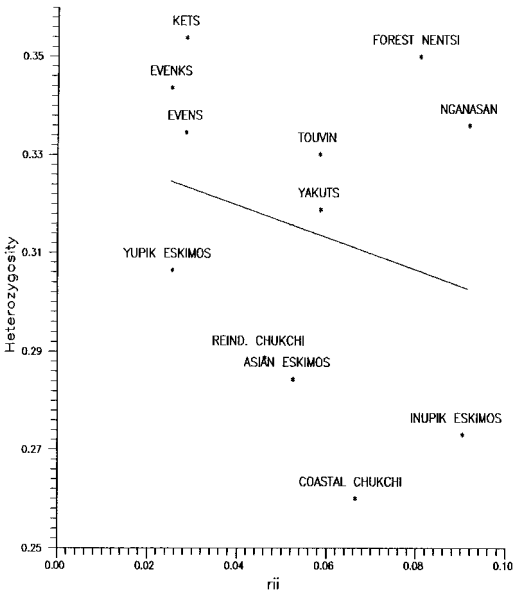

Fig. 6. A plot of the regression of heterozygosity (H) on the distance from the centroid of distribution (r_{ii}). The regression line shown is the theoretical one.

position between the Asian populations of Siberia and the Russians, reflecting gene flow from Russian populations.

Mantel tests

In Table 4, the correlations between genetics and geography, genetics and language, and geography and language are all significant. These correlations are not surprising when the geographic expanses of Siberia are considered as well as the possible roles that geographic barriers may have played in the evolution of languages and genetics during the Pleistocene (Rogers, 1986). The significant association between language and genetics disappears in the partial correlations when geography is kept constant. Yet the correlation between geography and genetics remains strong when language is kept constant. Using multiple correlation, the relationship between genetics and the combined effects of geography and language is high and significant. A total of 30.6% of variation in the genetics of Siberian populations is explained by the joint effects of language and geography. Judging from the moderate correlation between genetics and linguistics and the insignificant relationship between

genetics and linguistics when geography is kept constant, it appears that most of the genetic differentiation in Siberia is geographically patterned.

The Mantel tests have indicated a strong correlation of allele frequencies with geography and with linguistics, and the R-matrix analysis has identified meaningful groups of populations based on similarities in their allelic frequencies. Given that the allelic frequencies among Siberian indigenous populations are patterned geographically, it is desirable to examine the form of the patterning and identify the kinds of spatial processes implicated. Neither the Mantel tests nor the R-matrix analyses, can provide many insights into the character of the processes which spatially structure allelic frequency distributions.

Results of the spatial autocorrelation analysis are summarized in Table 5 for the following representative loci and alleles: GM*ZA;G, MN*M, ABO*A, FY*A, and RH*d. Reported for each spatial lag are: *N pairs*, the number of interpopulational comparisons involved in determining the level of spatial autocorrelation; Moran's **I**; and $\mathbf{p}_r$, the probability of $\mathbf{z}_r$ (the standardized (**z**-score) form of **I**) under a randomization model (Haggett et al., 1977).

Spatial correlograms are shown in Fig. 7A–E for the following loci and alleles: ABO*A, ABO*B, ABO*O (Fig. 7A); MNS*M, RH*d (Fig. 7B); GM*ZA;G, GM*ZAX;G, GM*ZABST, GM*F;B0135, KM*1 (Fig. 7C); ACP1*A, PGM*1, 6PGD*A (Fig. 7D); and FY*A, HP*1, P*P1 (Fig. 7E). In each figure the horizontal axis measures distance between populations (in kms); on the vertical axis the standardized (**z**-score) value of Moran's coefficient **I** at each spatial lag is plotted at the upper distance limit for the lag.

Several interesting patterns of spatial variation in allelic frequencies are indicated by the correlograms in Fig. 7A–E. The correlograms for the GM, KM, ACP, PGM, and 6PGD systems (Fig. 7C and 7D) illustrate an essentially monotonic decline in the level of spatial autocorrelation from large positive values at small spatial lags to large negative values at the largest spatial lags. Populations which are close geographically tend to have similar frequencies of a given allele, and populations which are widely separated tend to have different frequencies. The plots of these alleles represent the first law of geography. "Everything is related to everything else, but near things are more related than distant things" as stated by Tobler (1970). The steady decline exhibited by these correlograms is a clinal pattern on a continental scale of up to 7000 kms. Several of the GM haplotypes appear

TABLE 5. Spatial autocorrelation results for five blood markers

Marker	Spatial lag	n pairs	Moran's I	*P* (*r*)
ABO * A	1	183	0.2848	0.0213
	2	183	0.0543	0.2976
	3	183	0.0194	0.5957
	4	183	0.2521	0.0001
	5	183	0.0567	0.2456
	6	183	0.0021	0.7619
	7	183	0.0243	0.5375
	8	183	−0.0971	0.2292
	9	183	−0.4066	0.0000
	10	183	−0.2098	0.0009
RH * d	1	183	0.2973	0.0161
	2	183	0.2003	0.0014
	3	183	−0.1094	0.1713
	4	183	−0.0667	0.4607
	5	183	−0.1531	0.0303
	6	183	0.0888	0.0870
	7	183	−0.1711	0.0197
	8	183	−0.1270	0.0979
	9	183	−0.2651	0.0002
	10	183	0.2079	0.0001
MN * M	1	177	0.8872	0.0000
	2	177	−0.1887	0.0139
	3	176	−0.0757	0.3998
	4	178	−0.0667	0.4731
	5	177	−0.3087	0.0000
	6	177	0.1475	0.0089
	7	177	0.0381	0.4193
	8	177	0.0264	0.5249
	9	177	−0.5185	0.0000
	10	177	0.2906	0.0000
FY * A	1	96	0.3854	0.0003
	2	93	0.1374	0.0609
	3	95	0.0397	0.4629
	4	94	−0.2659	0.0050
	5	95	−0.5227	0.0000
	6	95	0.1603	0.0240
	7	94	−0.1757	0.0735
	8	95	−0.0180	0.9506
	9	94	0.0275	0.5495
	10	95	−0.0269	0.9629
GM * ZAG	1	61	0.7666	0.0000
	2	64	0.6824	0.0000
	3	64	0.5611	0.0000
	4	63	0.6431	0.0000
	5	63	0.5653	0.0000
	6	63	−0.6168	0.0000
	7	63	−0.7282	0.0000
	8	63	−0.4981	0.0000
	9	63	−0.7605	0.0000
	10	63	−0.8030	0.0000

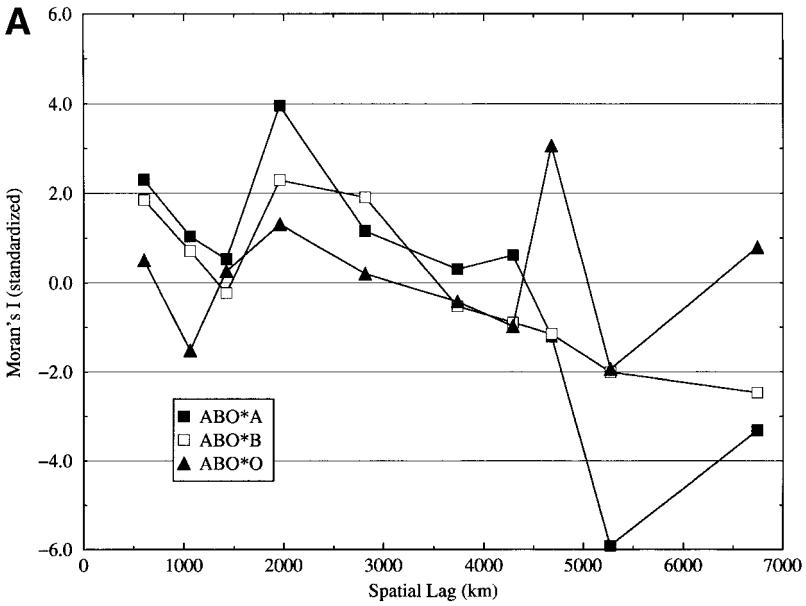

Fig. 7A. Correlogram for the ABO blood group system. The horizontal axis represents distance between populations (in kms.), while the vertical axis contains the standardized z-scores of Moran's coefficient I.

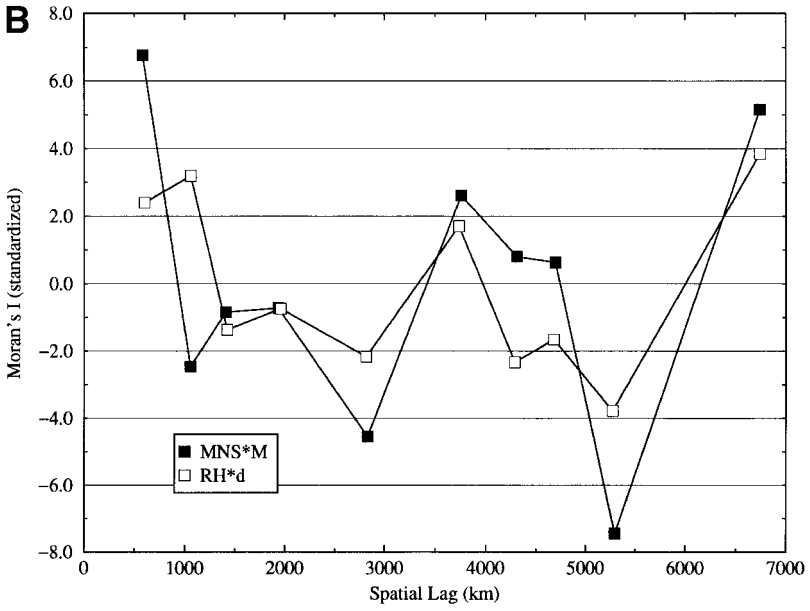

Fig. 7B. Correlogram for the MN and RH loci. The horizontal axis represents distance between populations (in kms.), while the vertical axis contains the standardized z-scores of Moran's coefficient I.

to be clinically distributed, GM*ZA;G, GM*FB and KM*1. GM*ZA;G also shows evidence of a sharp boundary beyond 2,500 km. However, GM*ZA;BST is different from the other GM haplotypes in showing a substantial rise in spatial autocorrelation with the largest lags, and is more similar to MN*M and RH*d than to other GM haplotypes.

The correlograms for the other alleles are less strikingly patterned but provide some light on the spatial processes that condition variation in alleleic frequencies. The correlograms for the systems Duffy (FY), haptoglobin (HPA), and P blood group (Fig. 7E) are similar in exhibiting high positive spatial autocorrelation at the smallest lags followed by a sharp decline to large negative values

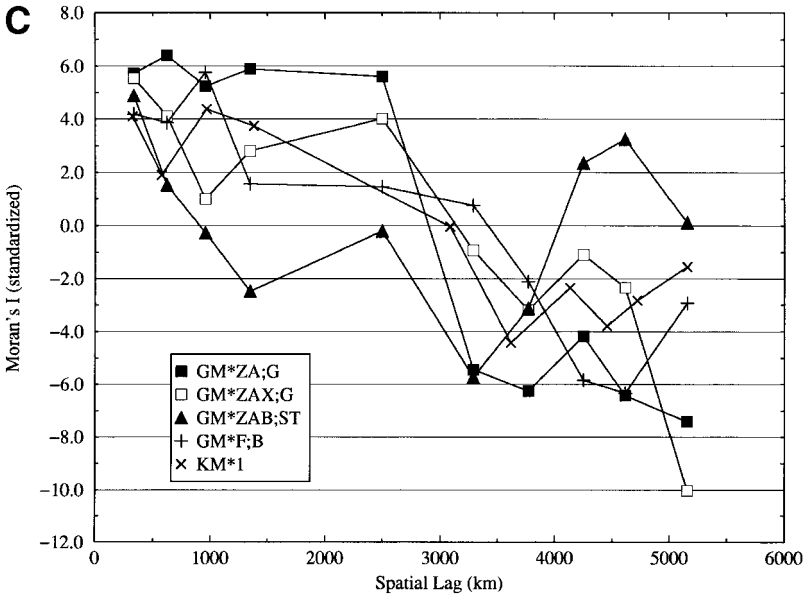

Fig. 7C. Correlogram for the GM and KM immunoglobulins. The horizontal axis represents distance between populations (in kms.), while the vertical axis contains the standardized z-scores of Moran's coefficient I.

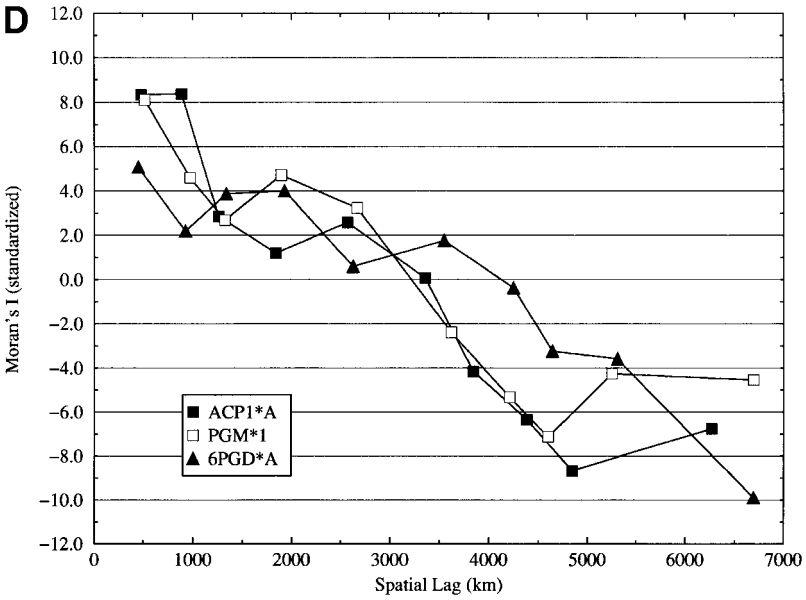

Fig. 7D. Correlogram for the acid phosphatase (ACP1), phosphoglucomutase (PGM), and 6-phospho-gluconate-dehydrogenase (PGD). The horizontal axis represents distance between populations (in kms.), while the vertical axis contains the standardized z-score of Moran's coefficient I.

at intermediate lags and essentially no spatial autocorrelation at the largest lags. These genetic systems thus exhibit strong small-scale clustering but are not spatially patterned over large, continental-scale distances as are the GM and KM haplotypes.

The correlograms for MN*M and RH*d (Fig. 7B) are provocative in exhibiting large positive values of spatial autocorrelation at the lowest and highest spatial lags, with small and fluctuating spatial autocorrelation at the intermediate lags. Thus, the closest and the most distantly separated populations tend to have similar frequencies of these alleles. Patterning of this kind could arise as a consequence of the historically documented migrations and invasions of Siberia, splitting a large genetically homoge-

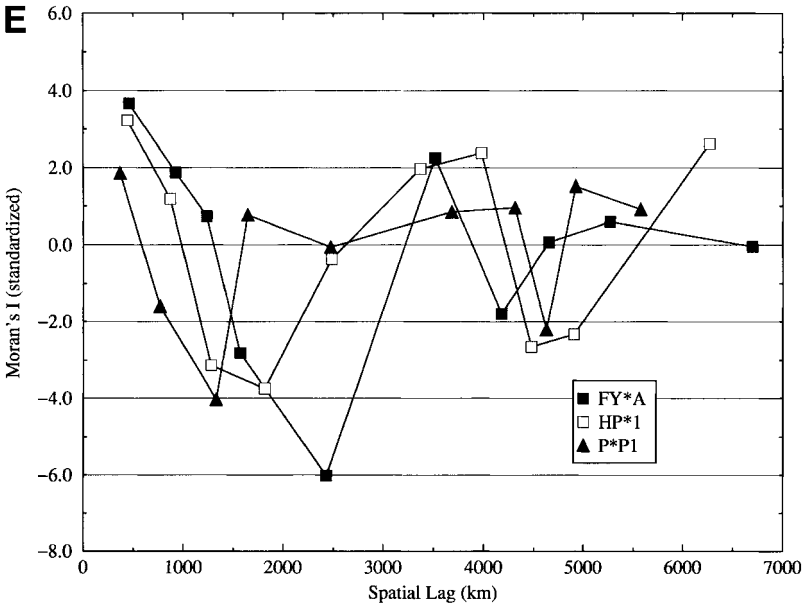

Fig. 7E. Correlogram for Duffy (FY), Haptoglobin (HP), and P systems. The horizontal axis represents spatial lag in kilometers, while the vertical axis contains the standardized z-scores of Moran's coefficient I.

neous population into two subgroups that have remained separated geographically. Apparently, genetic drift has not yet substantially altered the original similarity of their alleles.

Apart from some slight indications of local spatial clustering of allelic frequencies, the correlograms for the ABO system are unremarkable (see Fig. 7A). There is a hint in the correlograms for ABO*A and ABO*B of an isolation-by-distance effect (Malecot, 1948; Sokal and Wartenberg, 1983; Barbujani, 1987). However, these patterns are not as clearly expressed in the ABO system as they are in the GM and MN systems.

VNTRs and genetic structure

VNTRs are tandemly repetitive DNA loci that are found widely distributed throughout the human genome (Nakamura et al., 1987). Most VNTR loci vary in the number of short sequence repeats, although some loci are composed of more than one type of repeat (Jeffreys et al., 1991). The VNTRs are usually characterized by Southern blot hybridization or PCR techniques (Balazs et al., 1989; Budowle et al., 1991). During the last five years, frequency distributions of VNTRs have been successfully used to discriminate between populations from various geographic regions of the world (McComb et al., 1995a,b; Chakraborty et al., 1992; and Deka et al., 1992).

To date, the population structure of Siberian indigenous groups has been examined using VNTR distributions of five loci (D7S104, D11S129, D18S17, D20S15, and D21S112) by the University of Kansas research group in collaboration with Russian colleagues (McComb et al., 1995a). We have sampled populations of the Mountain Altai, Evenki, and Kets and have compared them to Native American, Mexican, American European and Afro-American populations (McComb et al., 1995b). R-matrix least-squares reduction plots revealed the clustering of Amerindian and Siberian populations while dramatically separating them from the Afro-American and the Euro-American groups (see Fig. 8). The first two eigenvectors account for almost 79% of the total variation observed. The first axis clearly separates the two synthetic populations (European American and African American) from the other groups. The second axis distinguishes the Afro-American group from the Euro-Americans. The most significant observation is the relatively tight clustering of the Siberian and Amerindian groups. On the basis of the VNTR distributions, the Mountain Altai

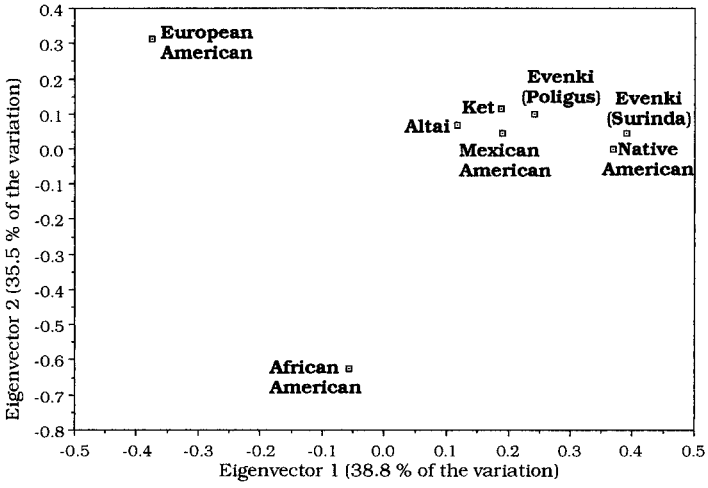

Fig. 8. Principal components analysis of the Siberian and American R-matrix using five VNTR loci (McComb et al., 1996).

population (Sokhon-Mindar) is almost indistinguishable from the Evenki populations.

CONCLUSION

After more than 30 years of research on the genetic structure of Siberian indigenous populations, using an assortment of analytical techniques and a variety of genetic markers, a number of conclusions about their geographic structure and phylogeny may be reached.

There is a clear-cut genetic kinship between Asian indigenous groups and Amerindian populations. Yet, it is difficult to attribute the origins of the Amerindians to a single Asian or Siberian group. The current mitochondrial DNA evidence and virological studies both suggest that the Mongolians and the Amerindians shared common ancestry (Merriwether et al., 1996; Neel et al., 1994). However, different regions of the genome (e.g., coding versus non-coding or Y-chromosome haplotypes vs. mtDNA) may have experienced unique evolutionary histories. Thus, it may be premature to assign the origins of New World populations solely on the basis of mtDNA and the presence of specific viral antibodies. The contact with Europeans has had profound genetic effects on both sides of the Bering Strait, through epidemics, warfare, and relocations of native peoples. These population dynamics make comparisons with contemporary populations difficult and the results are often ambiguous.

An intimate relationship exists between geography, linguistic, and genetic variation in Siberian groups. The glaciers of northern Siberia and the presence of Lake Mansi, played active roles in the geographic isolation and differentiation of languages and genetic distributions of Uralic, Altaic and Paleo-Asian speaking peoples. Although languages differentiated and resulted in the creation of linguistic families during the Pleistocene isolation, with the disappearance of the physical barriers the relationship between languages, geography and genetics became less pronounced. Relatively high correlations between distance matrices for geography, genetics, and linguistics persisted despite the fact that the relationship between these matrices is generally nonlinear.

Correlograms of gene frequency distributions for Siberian populations based upon spatial autocorrelation, correspond either to Malecot's isolation by distance model or are suggestive of a clinal pattern. The GM*ZA;G haplotype exhibits decreasing similarity with distance up to 3,000 km, beyond which the similarity drops rapidly. The loci that are most informative in discriminating among Siberian groups (PGM, ACP and PGD) follow in a linear or curvilinear fashion the diminution of similarity as a function of geographic distance.

The contemporary genetic structure of Siberian indigenous populations appears to be predominantly sculpted by the processes

of migration and stochastic processes. Gene flow was exacerbated by the forced collectivization of these groups during the 1930s plus the improvements in transport (such as railroads, helicopters and motorized boats), followed by greater mobility. Yet, many of these populations (such as the Evenki) have small effective sizes and continue to be geographically isolated.

Despite the determined efforts by Russian geneticists and anthropologists to measure genetic adaptation in Siberia, it is difficult to "mine" for natural selection in these small groups because of the combined effects of stochastic processes and sampling error. The action of natural selection has rarely been documented in human populations because of the "statistical noise" associated with small groups, and the necessity of selection coefficients of sufficiently high magnitude required for their detection.

ACKNOWLEDGMENTS

We thank Joe McComb who contributed greatly to the analyses of the data contained in this paper. This paper is dedicated to Derek F. Roberts, who started the senior author on the path of anthropological genetic research. The two junior authors may rightly claim "academic grandparenthood" of Derek Roberts.

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